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A new Amazonian species of *Adenomera* (Anura: Leptodactylidae) from the Brazilian state of Pará: a tody-tyrant voice in a frog

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ABSTRACT

Leptodactylid frogs are phenotypically diverse, widely distributed across the Neotropics, and are known to harbor high levels of cryptic species diversity. This is especially true in *Adenomera*, where several candidate species have been recognized in a genetics-based study. Here we describe a new Amazonian species of *Adenomera*, which corresponds to one of the lineages previously identified as a candidate species ("sp. F"). *Adenomera phonotriccus*, n. sp., differs from all 18 recognized congeners by its unique advertisement call. Moreover, this species can be distinguished from nearly all congeners (except *A. cotuba* and *A. lutzi*) in having antebrachial tubercles on the undersides of its forearms. The distribution of *A. phonotriccus* seems to be restricted to the Araguaia-Xingu interfluve, in the eastern portion of the Brazilian state of Pará. Additional sampling effort on the right margin of the Araguaia River and along the Xingu River drainage should clarify the distribution of *A. phonotriccus* and perhaps result in the discovery of additional undescribed species of *Adenomera* in a region with high biological diversity.

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INTRODUCTION

Adenomera Steindachner, 1867, is a Neotropical genus of leptodactylid frogs that is widespread in South America (east of the Andes), and currently comprises 18 valid and formally described species. However, many unnamed genetic lineages (i.e., candidate species) were identified by Fouquet et al. (2014) on the basis of multilocus phylogenetic analysis. The systematics of *Adenomera* is a complicated matter and more accurate species-level boundaries are better attained through the integrative use of multiple sources of evidence (Fouquet et al., 2014). To that end, acoustic and molecular evidence, in addition to morphology, have been increasingly employed to define the taxonomic status of several populations of this frog group (Angulo and Icochea, 2010; Carvalho and Giaretta, 2013a).

Here, we use an integrative approach to describe a new species of *Adenomera* from eastern Amazonia (Brazilian state of Pará). We assign the new taxon to one of the "confirmed candidate species" identified in the most recent and comprehensive phylogenetic hypothesis proposed for the genus (Fouquet et al., 2014)—assignment of the new species is based on mtDNA sequences obtained from type specimens.

Material and Methods

Study area and institutional acronyms: Fieldwork was conducted in the municipality of Palestina do Pará (5.70228° S latitude, 48.24949° W longitude, 166 m; datum WGS84), on the west margin of the lower Araguaia River, in the Brazilian state of Pará. Two expeditions to the area were conducted: (1) In 2010, one of us (P.L.V.P.) participated in an expedition to the area to inventory amphibians and reptiles. Several individuals of *Adenomera* were heard and collected at the time—some of these samples were included in the genetic study of Fouquet et al. (2014). At the time, specimens and tissue samples received different field numbers (DT for specimens, PV for tissue samples—these refer to Dante Pavan field numbers). Unfortunately, because the physical specimens collected in 2010 were not available for this study, only recordings and photographs of the specimens obtained by P.L.V.P. were used. (2) In January 2018, three of us (A.A., P.L.V.P., and T.R.C.) conducted a second expedition to the same locality to obtain additional specimens of *Adenomera*. We obtained four specimens of the new species, which compose the type specimens of the new taxon described below. We also collected additional specimens of two other *Adenomera* species.

Type specimens and additional specimens examined for comparisons are housed in the following Brazilian zoological/herpetological collections (see appendix 1 for details): Osvaldo Rodrigues da Cunha, Museu Paraense Emílio Goeldi (MPEG), Belém, Pará; Instituto Nacional de Pesquisas da Amazônia (INPA-H), Manaus, Amazonas; Paulo Bührnheim (CZPB-AA), Universidade Federal do Amazonas, Manaus, Amazonas; Museu de Biodiversidade do Cerrado (AAG-UFU), Universidade Federal de Uberlândia, Uberlândia, Minas Gerais; Universidade Federal de Minas Gerais (UFMG), Belo Horizonte, Minas Gerais; Célio F.B. Haddad (CFBH), Universidade Estadual Paulista, Rio Claro, São Paulo; Universidade de Brasília (CHUNB), Brasília, Distrito Federal; Museu de Zoologia da Universidade de São Paulo (MZUSP), São Paulo,

São Paulo; Museu de Zoologia da Universidade Estadual de Campinas (ZUEC-AMP), Campinas, São Paulo; Museu de Ciências e Tecnologia (MCP), Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, Rio Grande do Sul; Museu Nacional da Universidade Federal do Rio de Janeiro (MNRJ), Rio de Janeiro, Rio de Janeiro.

Morphology: Thirteen morphometric traits were measured from the four type specimens using a micrometric ocular piece (10 mm scale) coupled to a stereomicroscope (except SVL, measured with calipers) as follows: snout-vent length (SVL), thigh length (TL), shank length (SL), foot length (FL), tarsus length (TSL), hand length (HAL), forearm length (FRL), head length (HL), head width (HW), eye diameter (ED), tympanum diameter (TD), eye-nostril distance (END), internarial distance (IND). Head shape terminology follows that of Heyer et al. (1990). Morphological and color features follow the terminology of Heyer (1973). Morphometric definitions and terminology mostly follow those of Heyer et al. (1990); three measurements (ED, TD, and END) follow the definitions of Watters et al. (2016); head length (HL) corresponds to the distance between the tip of the snout and the midpoint (center) of the tympanum, head width (HW) corresponds to the distance between the midpoint of tympani.

Sound recordings and acoustic analysis: The species' vocalization was recorded in the study area (described earlier) using digital recorders (Marantz PMD 620, PMD 661, and PMD 670) set at a sampling rate of 44.1 or 48.0 kH and 16 bit sample size (mono WAVE file format), and Sennheiser K6/ME67 unidirectional microphones (those recorded with the PMD 620 were performed with a built-in microphone). Calls were analyzed using an interface built between Soundruler (Gridi-Papp, 2007) and Matlab (Matlab, 2004). Acoustic traits were quantified through automated analysis, for which we developed settings in the software to recognize and delimit the acoustic units in the time domain (notes, pulses, intervals, and pulse rate) and frequency domain (fundamental and dominant frequencies, and frequency modulation). Means and standard deviations of pulse duration and pulse interval for males recorded were obtained from mean values of these acoustic traits from each multipulsed call; the ranges included all raw measurements combined. Overall settings were: FFT size = 1024 samples, FFT overlap = 90%, window type = Hanning, contrast = 70%. Settings for automated recognition of pulses were: detection (smoothing = 120 samples, resolution = 12 samples); delineation (smooth factor = 1, smoothing = 25 samples, resolution = 1 sample); critical-amplitude ratio = -1 (disabled). Acoustic definitions and terminology are provided in appendix 2; information on sound recordings in appendix 3. Note rate (per minute) was quantified manually in Audacity v. 2.1.1 (Audacity Team, 2017). A 200 Hz high-pass filter at 48 dB was applied to sound files in Soundruler prior to conducting the acoustic analysis to reduce background noise; and a 500 Hz high-pass filter at 48 dB to file cuts used in the sound figures. Sound figures were obtained using seewave v. 2.1.0 (Sueur et al., 2008) and tuneR v. 1.3.2 (Ligges et al., 2017) in R v. 3.5.0 (R Core Team, 2018). Settings were: window Hanning, FFT size = 256 samples, FFT overlap = 90%.

The holotype of the new species (MPEG 41155) is one of the males recorded. Moreover, we recorded the vocalization of two paratopotypes (CFBH 43130–31) and one additional male

(not collected), but recordings of the latter three males were not included in the acoustic analysis because they were made in MP3 format. The paratopotype (MPEG 41156) was filmed while calling, but not recorded using adequate equipment. Even so, the distinct temporal envelope of the species call was aurally recognized in the field while recording calling males, and then confirmed in Audacity. In 2010, P.L.P.V. recorded (wave files) two males at the type locality: PLPDR 096–098 (voucher field no. DT 2123) and PLPDR 100 (voucher field no. DT 2133). The voucher specimen (DT 2123) is referred by its tissue sample number (PV 2597) in Fouquet et al. (2014: appendix 1). The best recording (PLPDR 100) was included in the acoustic analysis. Both recordings from 2010 have associated vouchers, but we could not examine the specimens given that they are not yet housed in any zoological collection.

Comparative acoustic data for other *Adenomera* species are summarized in table 3. The call described for *Adenomera andreae* from French Guiana (Boistel et al., 2006) agrees with unpublished calls of topotypes of this species (Carvalho et al., in prep.) and were regarded as nominal *A. andreae* calls. The call of *A. diptyx*, however, is poorly characterized in the literature. The only call descriptions that could be assigned to nominal *A. diptyx* were published by Márquez et al. (1995). These authors provided data on *A. diptyx* from Bolivia, reported as *A. andreae* though (De la Riva, personal commun. to A.A.). Also, pulse number was not quantified for the species. It is worth mentioning that a taxonomic review of *A. diptyx* is in progress (Zaracho, personal commun.). Superficially, the *A. diptyx* call (Carvalho, unpubl. data) can be characterized by being pulsed (few pulses per note), having short duration (~50 msec), and emitted at a high rate (> 100 notes/min.).

DNA Sequencing and phylogenetic analysis: We assembled a matrix of mtDNA cytochrome oxidase subunit I (COI) sequences from GenBank for all individuals from the appendix S1a of Fouquet et al. (2014) and added new sequences for the four type specimens of the new species. GenBank accession numbers for the new species are as follows: MK188928 (paratype, CFBH 43130), MK188929 (paratype, CFBH 43131), MK188930 (holotype, MPEG 41155), MK188931 (MPEG 41156).

For newly generated sequences, genomic DNA was extracted from ethanol-preserved muscle tissue using standard ammonium acetate extraction protocol adapted from Maniatis et al. (1982). Primers employed for amplification (COI gene) and PCR enzymatic reaction conditions follow those of Lyra et al. (2017), and the resulting amplified fragments were sequenced by Macrogen Inc. (Seoul, South Korea). Chromatograms were checked manually, assembled, and edited using Geneious v. 7 (Biomatters Ltd.).

We performed multiple sequence alignment using Muscle option in MEGA v. 7 (Kumar et al., 2016). Then, we used PartitionFinder v. 2.1.1 (Lanfear et al., 2017) to select the optimal partition scheme and nucleotide substitution models using linked model of branch lengths with greedy search algorithm. For this analysis, we previously defined three partitions. The best model was selected through Bayesian information criterion (BIC). We conducted a Bayesian phylogenetic inference analysis using MrBayes v. 3.2.6. (Ronquist et al., 2012), implemented in the online CIPRES Science gateway portal (Miller et al., 2010), with two independent runs of 1.0×10^7 generations, with four Markov chains (one cold), sampled every 1000 generations.

We discarded 25% of generations and trees as burn-in and performed the run with unlinked character state frequencies, substitution rates under SYM+I+G, HKY+I, and GTR+G models for the three partitions, respectively. We verified the convergence and minimal effective sample sizes (ESS >200) of the parameters in Tracer v. 1.6 (Rambaut et al., 2014).

SPECIES ACCOUNT

Leptodactylidae Werner, 1896

Adenomera Steindachner, 1867

Adenomera phonotriccus, n. sp.

Figures 1–3

Referred material: Voucher specimens with DNA sequenced by Fouquet et al. (2014) and assigned to *Adenomera* sp. F (in part).

Suggested vernacular name: Tody-tyrant-voiced nest-building frog.

Holotype: MPEG 41155 (field number TRC 135), adult male, from the municipality of Palestina do Pará (5.70228° S, 48.24949° W; 166 m), on the western margin of the lower Araguaia River, state of Pará, northern Brazil, collected by P.L.V. Peloso, M.J. Sturaro, P.V. Cerqueira, G. Gonçalves, A.A. Giaretta, P. Marinho, and T.R. de Carvalho on January 9, 2018 (Zoobank LSID registration: urn:lsid:zoobank.org:act:330AE4AB-1ABB-4B90-9245-1DBC2A1F661B).

Sound recording: Adenomera_phonotriccusPalestinaPA2bAAGm661MK2.

Paratopotypes: MPEG 41156 and CFBH 43130–43131, all adult males, collected (5.70300° S, 48.24833° W; 176 m) on January 9–10, 2018, by the same collectors.

Etymology: The epithet *phonotriccus* is the combination of Greek *phono-* (from *phoné*, "sound, voice") and *triccus* (a small bird whose species is not identifiable, though in modern times the name is applied to tyrant flycatchers; Jobling, 2010). This name is to be treated as a noun in apposition and is an allusion to the similarity between the vocalization of the new species and those of tody-tyrants. Tody-tyrants of the Neotropical genus *Hemitriccus* have peculiar vocalizations, which are reminiscent of the vocalization of *Adenomera phonotriccus*, especially the trilled song of *H. cohnhafti* (see Zimmer et al., 2013). Interestingly, several *Hemitriccus* species are morphologically very similar, and consequently best differentiated by their vocalizations, a pattern also observed in *Adenomera*.

Diagnosis: *Adenomera phonotriccus* is differentiated from its congeners by the following combination of characters: (1) small size (adult male SVL 19.8–21.6 mm; table 1); (2) robust body shape; (3) toe tips unexpanded to slightly swollen (character states B, C; Heyer, 1973); (4) distal antebrachial tubercle on underside of forearm; (5) throat and belly cream colored, mottled white and gray in some parts; (6) two color morphotypes (presence/absence of dorsolateral stripes); (7) advertisement call consisting of a single type of pulsed note, emitted regularly, not in calling bouts; (8) advertisement notes composed of complete pulses (pulses with periods of silence in between); (9) long-lasting call duration (213–433 ms).

TABLE 1. Morphometric measurements (in mm) for the type series of *Adenomera phonotriccus*. Abbreviations are defined in the Materials and Methods. * Holotype.

Measurements	*Adenomera phonotriccus*, n. sp. (N = 4 adult males)					
	MPEG 41155*	MPEG 41156	CFBH 43130	CFBH 43131	Mean ± SD	Min-Max
SVL	20.8	20.6	19.8	21.6	20.7 ± 0.7	19.8–21.6
HL	6.6	6.6	6.2	6.8	6.6 ± 0.3	6.2–6.8
HW	7.7	7.9	7.7	7.9	7.8 ± 0.1	7.7–7.9
ED	1.8	2.0	1.8	2.1	1.9 ± 0.2	1.8–2.1
TD	1.7	1.5	1.1	1.3	1.4 ± 0.3	1.1–1.7
END	1.6	1.5	1.4	1.5	1.5 ± 0.1	1.4–1.6
IND	1.8	1.6	1.9	2.0	1.8 ± 0.2	1.6–2.0
HAL	4.6	4.4	4.9	5.0	4.7 ± 0.3	4.4–5.0
FRL	3.5	3.8	4.1	4.2	3.9 ± 0.3	3.5–4.2
TL	8.8	9.2	9.1	9.0	9.0 ± 0.2	8.8–9.2
SL	8.3	8.5	8.8	9.0	8.7 ± 0.3	8.3–9.0
TSL	4.9	4.3	4.7	5.0	4.7 ± 0.3	4.3–5.0
FL	9.3	9.1	8.8	9.9	9.3 ± 0.5	8.8–9.9

COMPARISONS: *Adenomera phonotriccus* has adult males (SVL 19.8–21.6 mm; table 1) smaller than those of *A. coca* (23.6–25.6 mm; Angulo and Reichle, 2008), *A. lutzi* (25.7–33.5 mm; Kok et al., 2007), and *A. simonstuarti* (SVL 25.9–26.2 mm; Angulo and Icochea, 2010). *Adenomera phonotriccus* has a robust body shape (figs. 1–2), whereas *A. diptyx, A. martinezi,* and *A. saci* have a slender body (Carvalho and Giaretta, 2013a). *Adenomera phonotriccus* has toe tips unexpanded or slightly swollen (character states B, C), but not expanded into flattened discs (character state D) as in *A. ajurauna, A. andreae, A. marmorata, A. lutzi, A. nana*, and *A. simonstuarti* (Angulo et al., 2003; Kok et al., 2007; Kwet, 2007; Berneck et al., 2008; Angulo and Icochea, 2010; appendix 1). *Adenomera phonotriccus* is distinguished from congeners (except *A. cotuba* and *A. lutzi*; Kok et al., 2007; Carvalho and Giaretta, 2013b) by having antebrachial tubercles on underside of forearm (fig. 3), presumably absent in all remaining species. *Adenomera phonotriccus* differs from *A. heyeri* and *A. lutzi* by having ventral surfaces cream colored (mottled white and gray in some parts), yellow in the latter two species (Boistel et al., 2006; Kok et al., 2007). From *A. engelsi*, which does not have distinctive dorsolateral stripes and pigmentation on throat (Kwet et al., 2009), *Adenomera phonotriccus* differs by the occurrence of both color features (fig. 1). *Adenomera cotuba* does not have dorsolateral stripes (Carvalho and Giaretta, 2013b), whereas *A. phonotriccus* has two color morphotypes (presence/absence of dorsolateral stripes). These species are better distinguished by their distinct vocalizations (see below; fig. 4).

The advertisement call of *Adenomera phonotriccus* (fig. 4; table 2) distinguishes it from all congeners by having pulsed notes composed of complete pulses (periods of silence in between), whereas the other species' notes are formed by incomplete pulses, i.e., not separated one from the next by periods of silence (fig. 4). From the remaining species of *Adenomera*, the new spe-

TABLE 2. Advertisement-call traits for the holotype (MPEG 41155), one additional male (field # DT 2133), and one unvouchered male of *Adenomera phonotriccus*. Sound recordings were obtained at the species' type locality (Palestina do Pará, state of Pará, northern Brazil). Values are means ± SD (min-max). Zeros in ranges comprise rounded values (lower than 0.5 ms).

Call traits	MPEG 41155	Unvouchered	Field # DT 2133	Grand mean ± SD
Note duration (msec)	393.0 ± 17.6 (370–433) N = 15	294.4 ± 30.2 (213–361) N = 79	267.5 ± 16.1 (230–293) N = 26	318.3 ± 66.0 (213-433) N = 120
Note rate/min	22.1 N = 1	30.8 ± 6.6 (26–35) N = 2	33.1 ± 2.9 (31–35) N = 2	28.6 ± 5.8 (26-35) N = 5
Note rise time (%)	72.8 ± 5.7 (66–84) N = 15	63.2 ± 10.3 (43–85) N = 79	72.5 ± 5.0 (60–80) N = 26	69.5 ± 5.5 (43-85) N = 120
Pulses per note	23.5 ± 1.1 (22–26) N = 15	17.7 ± 1.1 (14–22) N = 79	15.7 ± 0.8 (14–17) N = 26	19.0 ± 4.0 (14-26) N = 120
Pulse duration (msec)	7.8 ± 0.3 (4–13) N = 352	8.9 ± 1.5 (4–26) N = 1398	7.4 ± 0.4 (4–13) N = 408	8.0 ± 0.8 (4-26) N = 2158
Pulse silence (msec)	9.3 ± 0.3 (6–12) N = 337	8.1 ± 0.6 (0–13) N = 421	10.3 ± 0.5 (7–17) N = 382	9.3 ± 1.1 (0-17) N = 1140
Pulse rate/sec	58.3 ± 0.6 (58–60) N = 15	59.6 ± 4.9 (51–67) N = 79	56.5 ± 1.1 (55–59) N = 26	58.1 ± 1.6 (51-67) N = 120
Fundamental frequency (Hz)	1980.0 ± 6.9 (1966–1990) N = 15	1942.2 ± 29.0 (1857–1997) N = 79	1959.8 ± 24.2 (1876–1982) N = 26	1960.7 ± 18.9 (1857-1997) N = 120
Dominant frequency (Hz)	4026.7 ± 16.3 (3984–4070) N = 15	3858.7 ± 131.0 (3639–4008) N = 79	4051.6 ± 40.7 (3898–4113) N = 26	3979.0 ± 104.9 (3639-4113) N = 120
Linear freq. modulation (Hz)	456.5 ± 216.4 (0–861) N = 15	265.3 ± 165.2 (-43–603) N = 79	551.6 ± 146.2 (129–732) N = 26	424.5 ± 145.8 (-43-861) N = 120

cies differs by having pulsed advertisement notes, whereas those species' calls consist of non-pulsed notes (table 3). The advertisement call of *A. phonotriccus* is distinguished from that of *A. cotuba* by being composed of single notes emitted regularly (table 2), whereas *A. cotuba*'s call is made up of many notes emitted as calling bouts, i.e., multinote advertisement call (Carvalho and Giaretta, 2013b: fig. 4A). In addition, to date, *Adenomera phonotriccus* has the longest note duration in the genus, whose range does not overlap with note-duration values for any congeners (table 3).

Description of holotype: MPEG 41155 (figs. 1A, 2, 3A). Adult male. Body robust (figs. 1A, 2A). Snout subovoid in dorsal view (fig. 2A), acuminate in lateral view (fig. 2D). Nostrils closer to the snout tip than to the eyes; fleshy ridge on snout tip; *canthus rostralis* not marked; loreal region slightly concave; supratympanic fold from the posterior corner of the eye to the base of the arm; oval postcommissural gland; vocal sac subgular with a fold from jaw extending to forearm on each side, vocal slits present; vomerine teeth in two straight rows medial and posterior to choanae and oblique to sagittal plane. Tongue elongated, free behind. Relative finger lengths IV < I < II < III; fingers without ridges or fringes; finger tips rounded, slightly expanded, but not flattened; inner metacarpal tubercle nearly rounded; outer metacarpal tuber-

TABLE 3. Acoustic information on *Adenomera* with special reference to advertisement-call (= note) duration, pulses (presence/absence), peak frequencies in the first two harmonics. Abbreviations: N = nonpulsed; H0 = 1st harmonic; H1 = 2nd harmonic.

Species	Note duration (msec)	Pulses/ note	H0 frequency (kH)	H1 frequency (kH)	Reference
A. ajurauna	130–190	N	3.72–5.43	—	Berneck et al. (2008)
A. andreae[a]	45–86	4	2.32–2.69	4.56–5.49	Boistel et al. (2006)
A. araucaria	86–140	5–11	1.72–3.36	4.63–5.40	Kwet and Angulo (2002)
A. bokermanni[b]	99–152	N	1.79–1.83	3.40–3.57	Kwet (2007)
A. coca	110–145	10–15	1.69–1.91	3.45–3.75	Angulo and Reichle (2008)
A. cotuba	69–191	8–14	1.73–1.83	3.33–3.80	Carvalho and Giaretta (2013b)
A. diptyx[c]	56–88	Pulsed	2.18–2.28	4.20–4.50	Márquez et al. (1995)
A. engelsi	96–163	N	ca. 2000	3.46–4.29	Kwet et al. (2009)
A. heyeri[a]	137–185	9.5	1.82–1.88	3.57–3.84	Boistel et al. (2006)
A. hylaedactyla	35–62	4–6	1.95–2.21	3.96–4.48	Angulo et al. (2003)
A. juikitam	148–202	16–21	1.88–2.11	3.70–4.17	Carvalho and Giaretta (2013b)
A. lutzi	41–61	N	1.64–1.81	3.27–3.62	Kok et al. (2007)
A. marmorata[d]	100	N	4.50–5.60	—	Straughan and Heyer (1976)
A. martinezi	63–151	15–21	1.88–2.06	3.38–4.13	Carvalho and Giaretta (2013a)
A. nana	67–122	N	2.30–2.70	4.62–5.44	Kwet (2007)
A. phonotriccus, n. sp.	213–433	14–26	1.86–2.00	3.64–4.11	This study
A. saci	90–241	N	1.69–2.25	3.38–4.41	Carvalho and Giaretta (2013a)
A. simonstuarti	57–71	3–4	1.81–2.03	3.71–4.05	Angulo and Icochea (2010)
A. thomei	120–210	10–21	2.15–2.81	4.57–5.56	Almeida and Angulo (2006)

[a] Sinusoidal oscillation (Boistel et al., 2006) corresponds to incomplete pulses in *Adenomera*, based on (quasi-) periodic sinusoidal FMs (sometimes there is strong modulation unaccompanied by distinct pulses though).
[b] Based on the call of *Adenomera* sp. 2 from Joinville.
[c] See Materials and Methods for a detailed explanation.
[d] Frequencies lower than 1 kH do not pertain to this species' call (appendix 2).

cle rounded (fig. 3A). Subarticular tubercles rounded; supernumerary tubercles discrete, rounded. Antebrachial tubercle on distal end of forearm. Dorsum shagreened, warty on flanks and inguinal region. Throat and center of belly smooth (fig. 2B). Belly granular laterally and posteriorly. A pair of lumbar glands on sacral region. Ventral surface of thighs granular. Posterior surface of thighs with no distinctive pattern, possessing discrete and rounded paracloacal glands. Relative toe lengths I < II < V < III < IV; toes without ridges or fringes; toe tips rounded

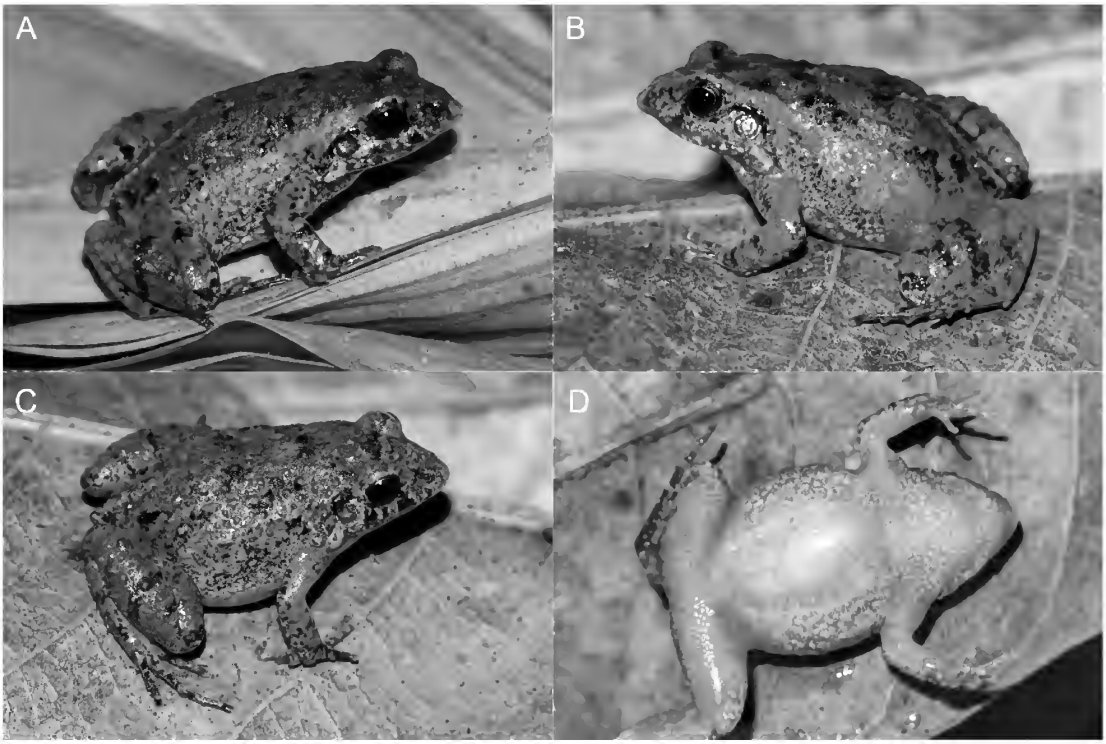

FIG. 1. Live specimens (all adult males) of *Adenomera phonotriccus* from the type locality (Palestina do Pará, state of Pará, northern Brazil). **A,** Holotype (MPEG 41155). **B,** Paratopotype CFBH 43130. **C–D,** Paratopotype CFBH 43131.

and slightly swollen in toes II–IV. Inner metatarsal tubercle oval, outer metatarsal tubercle rounded (fig. 3C). Tarsal fold from the inner metatarsal tubercle extending 1/2 length of tarsus. Subarticular tubercles rounded or subconical; supernumerary tubercles rounded, discrete. Measurements of the holotype are provided in table 1.

Color of holotype in preservative (fig. 2): Snout tip with a faded white coloration (coincident with the fleshy ridge). Dorsum marble gray with a few darker specks and spots. Sacral stripe on the posterior third of body length, cream-colored. Black lumbar glands. Dorsal surface of limbs with dark brown stripes/blotches on a slightly lighter brown background. Dorsolateral, broad stripe from the posterior corner of the eye, passing over the flanks, predominantly cream-colored to a somewhat orange hue (faded coloration; orange in life). Upper and lower jaws covered with white-colored spots/blotches, whitish postcommissural gland, outlined at the bottom by a dark coloration. Tympanum reddish brown. Throat, belly, and ventral surface of limbs cream, with melanophores, throat with a black-dotted pattern, solid dark-colored laterally, coinciding with the expanded vocal sac. Posterior surface of thighs with a few dark brown spots on a light brown background, and paracloacal glands cream colored.

Color of holotype in life (fig. 1A): Dorsum covered with black specks and spots irregularly distributed on medium brown background. Arms and legs reddish brown. Sacral and

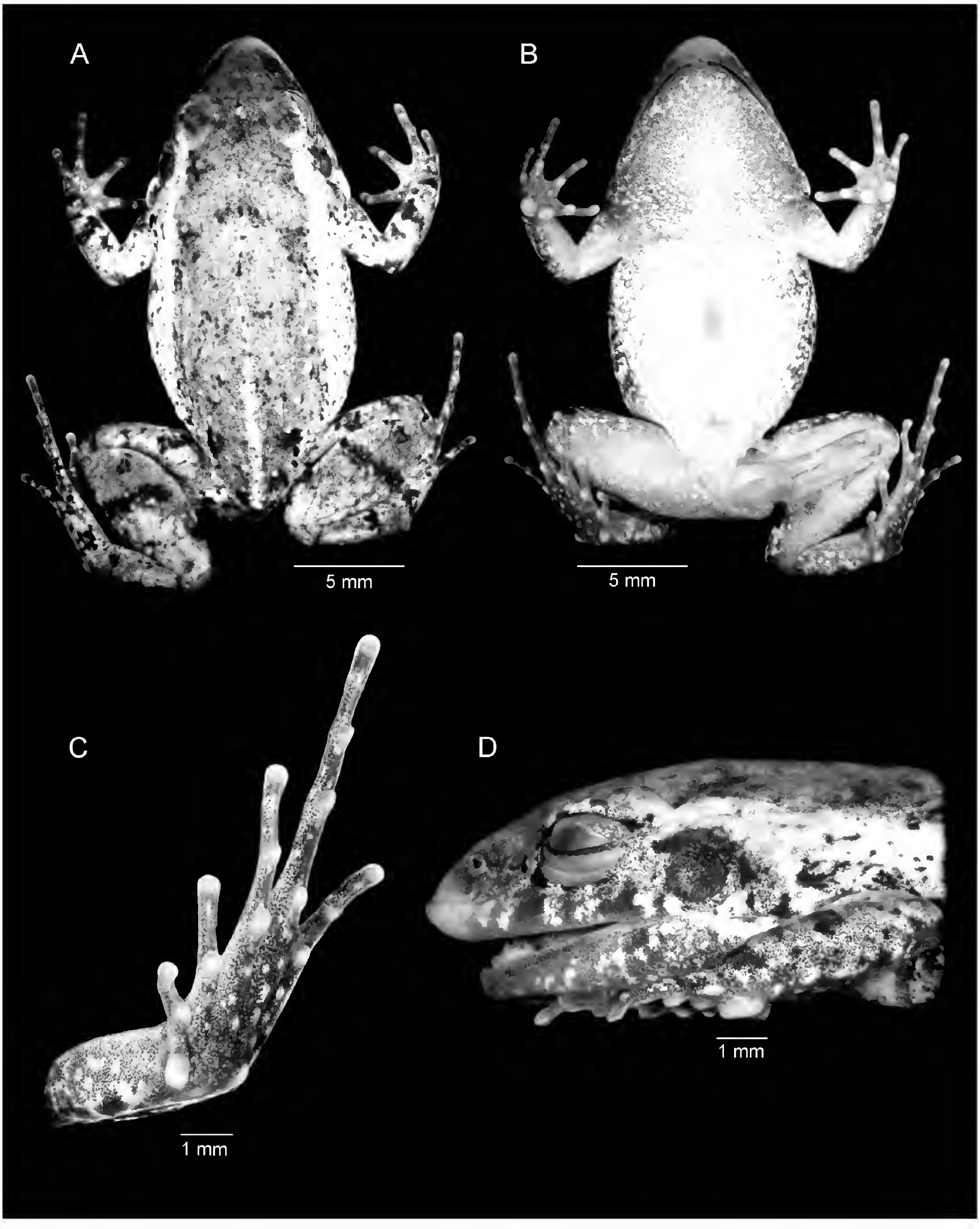

FIG. 2. Preserved holotype of *Adenomera phonotriccus* (adult male, MPEG 41155; SVL 20.8 mm). **A,** Dorsal body. **B,** Ventral body. **C,** Sole of foot. **D,** Lateral head.

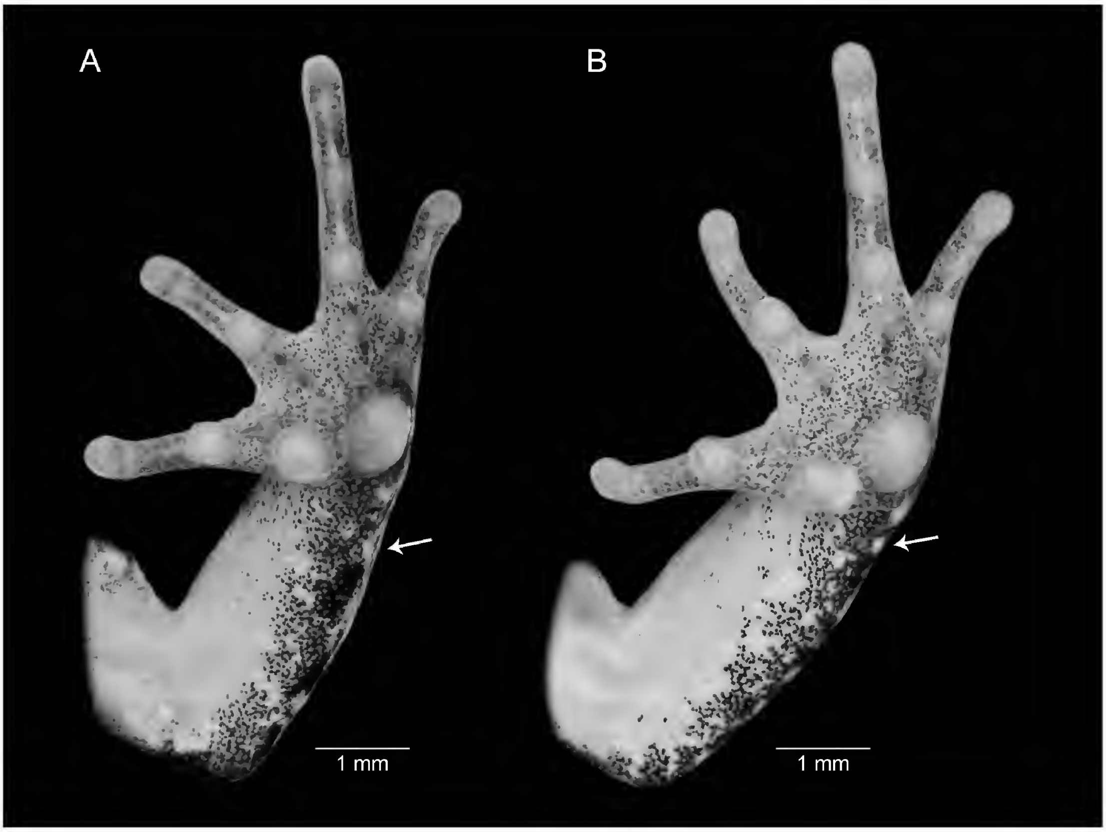

FIG. 3. Antebrachial tubercle in type specimens of *Adenomera phonotriccus*. **A,** Holotype (adult male, MPEG 41155). **B,** Paratopotype (adult male, CFBH 43131). The white arrows indicate the position of tubercles on distal edge of the forearm.

dorsolateral stripe, and postcommissural gland orange. Iris copper. Tympanum brown. Ventral surfaces cream colored and with mottling on throat and belly (laterally). Groin yellow.

Variation in the type series: Despite minor variation in dorsal coloration and distribution of spots, specks, and warts on dorsal surfaces, characteristics of the three paratypes largely agree with the description of the holotype. Dorsolateral stripe is absent in two paratypes (MPEG 41156 and CFBH 43130). Shape and size of antebrachial tubercle varies among the type series; some of them are very discrete (fig. 2).

Advertisement call: The description is based on recordings of three males (appendix 3). Sample sizes for each acoustic trait and descriptive statistics, i.e., means and standard deviations, are provided in table 2. The call (fig. 4) consists of a single type of pulsed note, which is emitted at a rate of 26–35 calls per minute. Note duration varies from 213–433 msec. Notes have a smooth attack and decay, reaching the amplitude peak at 43%–85% of their duration. Pulse number varies from 14–26; pulse duration from 4–26 msec, emitted at a rate of 51–67 pulses per second; silence between pulses varies from nearly zero to 13 msec. The fundamental frequency of the note occupies a narrow bandwidth harmonic, with a peak frequency of 1857–

1997 Hz; the dominant frequency varies from 3639–4113 Hz and is contained within the second harmonic. Notes usually have a slight positive frequency modulation along their duration, but a few notes do not have any modulation, and a single note has negative modulation. Linear frequency modulation varies from -43–861 Hz.

Habitat and natural history: *Adenomera phonotriccus* is associated with forest habitats in Brazil's eastern Amazonia in the state of Pará. The type locality is located on the west margin of the lower Araguaia River. This region is also occupied by savanna landscapes or ecotones between the Cerrado and Amazonian rainforest. The species was heard along an open area transect (by recent logging activity), especially at the forest edge, and inside the forest remnant. Males called while exposed or under leaf litter, and increased their calling activity during and shortly after rainfalls. The vocalization of *Adenomera phonotriccus* is very peculiar when heard in the field. Our first impression was that the calls might not be produced by a leptodactylid frog, or even an anuran species. Indeed, the vocalization is similar to that of some Neotropical suboscine birds (e.g., Rhynchocyclidae, Tyrannidae). There were two partially syntopic species of *Adenomera* also in calling activity at the study site: *Adenomera* sp. (*A. heyeri* clade) and *A.* aff. *hylaedactyla*. We heard the three species calling at the same period (late afternoon), even though *A. phonotriccus* and *Adenomera* sp. ceased most calling activity at dusk, whereas *A.* aff. *hylaedactyla* continued calling through the first hours of the night. The last species occupied open areas, e.g. pasture. In contrast, *A. phonotriccus* and *Adenomera* sp., are associated with forest habitats.

Distribution (fig. 5): *Adenomera phonotriccus* is known with certainty only from the type locality and Marabá. However, specimens from other regions in the state of Pará were also assigned to this lineage, referred as *Adenomera* sp. F, by Fouquet et al. (2014). Given the high levels of cryptic species diversity in *Adenomera* and complex genetic structure within the lineages identified by Fouquet et al. (2014), we conservatively restrict the species' distribution to the type locality region until additional data, especially vocalizations, are obtained for the other populations assigned to *Adenomera* sp. F, a lineage widely distributed in central-east Pará, northern Brazil.

Conservation status: Because the species is apparently restricted to forested habitats, or its immediate margins (forest edge), we infer that the current population trend for this species is "declining." Major threats are deforestation (destruction of habitats) due to conversion of large areas where the species occur into pasture and agricultural land. The species appears to be locally abundant (although difficult to observe), which means that as long as its habitat is preserved the species should have its future secured. The known range of the species is hard to determine with current evidence. It may be much wider, if all the clade F specimens refer to *A. phonotriccus,* in which case the species would be found from the western margin of the Tocantins River to the western margins of the Tapajós River (Fouquet et al., 2014: fig. 2). Alternatively, it could have a much narrower distribution (southern Pará) if only specimens in subclade F3 correspond to *A. phonotriccus*—in the latter case, the species would be probably restricted to small forest fragments in one of the most highly threatened portions of the Amazonia (the so-called Arc of Deforestation). This is a typical example of the issues raised by

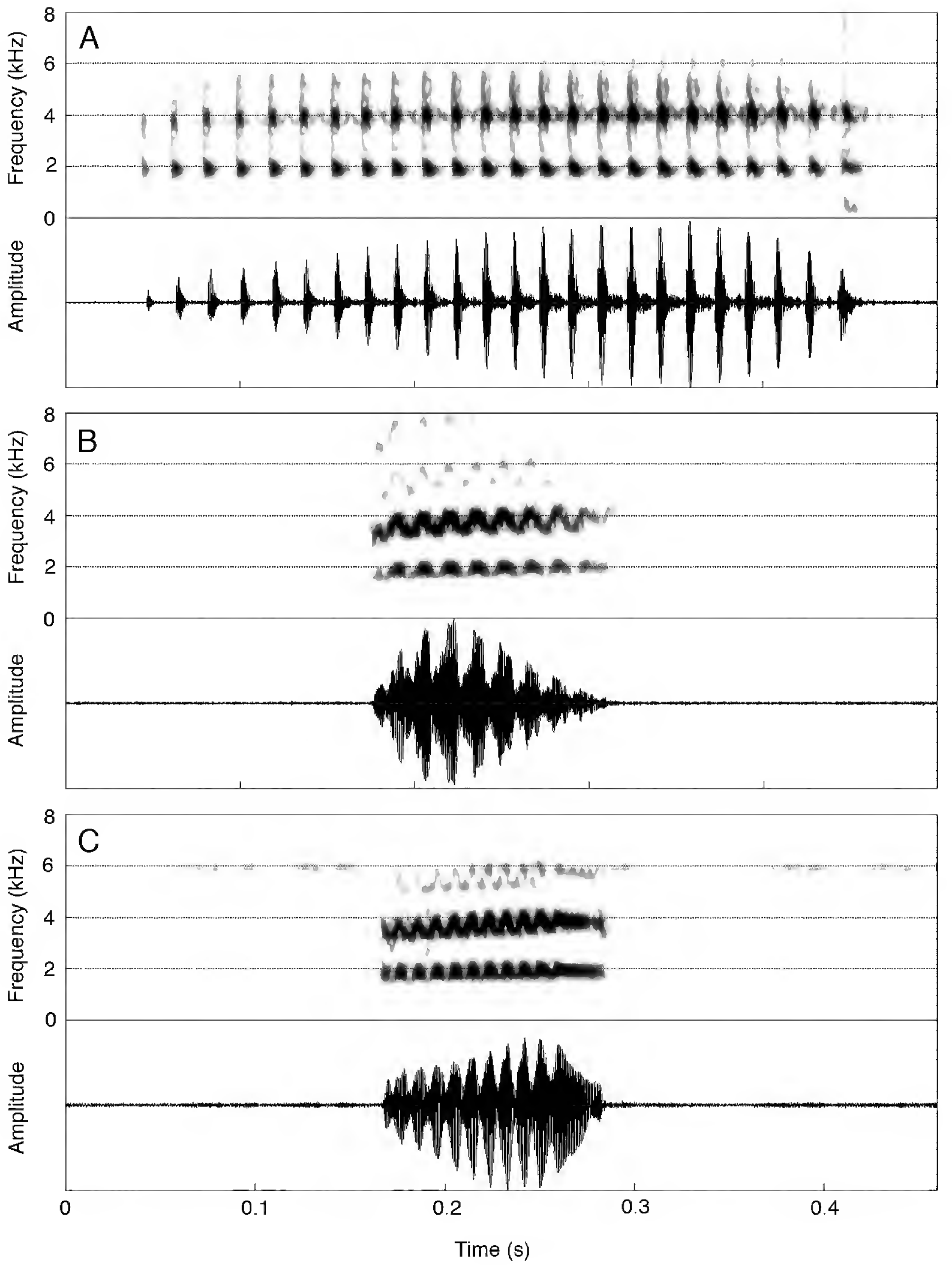

FIG. 4. Advertisement calls of three *Adenomera* species. **A,** *Adenomera phonotriccus* from the type locality (Palestina do Pará, Brazil), recorded by A.A. Giaretta (holotype, MPEG 41155): a note containing 24 complete pulses. **B,** *Adenomera heyeri* from Mont Itoupé (French Guiana), recorded by A. Fouquet (AF 3547): a note containing 9 incomplete pulses. **C,** *Adenomera cotuba* from the type locality (Teresina de Goiás, Brazil), recorded by T.R. de Carvalho (paratype, AAG-UFU 1397): a note containing 10 incomplete pulses from a 26 note call. Spectrograms and oscillograms were produced on the same time scale (ca. 0.5 sec). The intensity of frequency components is indicated by their darkness in a relative 40 dB scale.

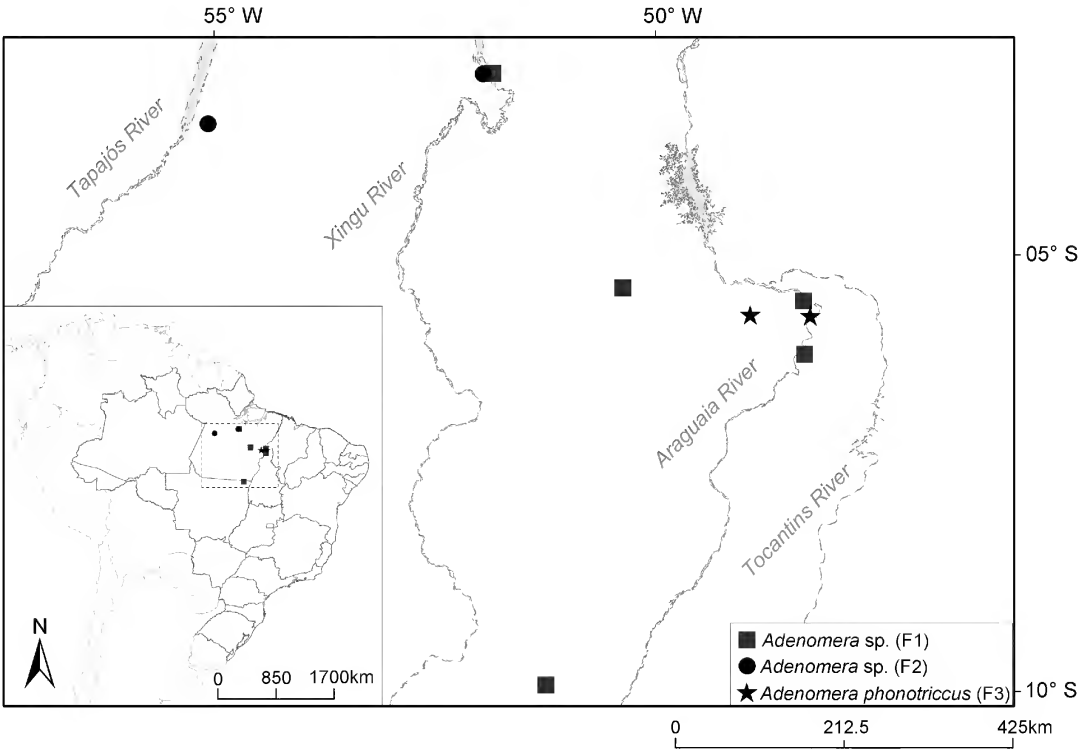

FIG. 5. Geographic distribution for the three clades within the Amazonian lineage F of *Adenomera* of Fouquet et al. (2014): *A. phonotriccus* (subclade F3), and subclades *Adenomera* F1 and F2.

Peloso (2010) and Angulo and Icochea (2010), where lack of taxonomic resolution hinders a proper assessment of threats to cryptic species. For now, we must unfortunately suggest this new species is yet another case of data-deficient taxa—a lot more studies and data are needed to define the conservation status of *A. phonotriccus*.

Remarks: Calls of the voucher PV 2597 (specimen no. DT 2123; recordings PLPDR 100; see appendix 3) were unambiguously assigned to *A. phonotriccus* ("F3" in fig. 6). This voucher was cited as collected in Araguatins (state of Tocantins), on the east margin of Araguaia River. However, this specimen was actually collected in Palestina do Pará, state of Pará—the animal was collected by P.L.V.P. in 2010 (coordinates given by Fouquet et al.'s appendix 1 are correct). The basecamp for this collection site was in Araguatins, and this may have been the source of confusion with the sample provenance (P.L.V.P., personal obs.). Another voucher specimen used in the phylogeny (PV 2412, specimen no. DT 2016), also assigned here to *A. phonotriccus* ("F3" in fig. 6) was collected in Marabá—this municipality is located in the state of Pará, not Amazonas (AM), as mentioned in appendix 1 of Fouquet et al. (2014).

Of special interest is the acquisition of additional information for the subclade F1, which occurs in partial sympatry with *A. phonotriccus* (fig. 6). Meanwhile, we conservatively assign only subclade F3 (sensu Fouquet et al., 2014) to *A. phonotriccus*, and this species is an endemic

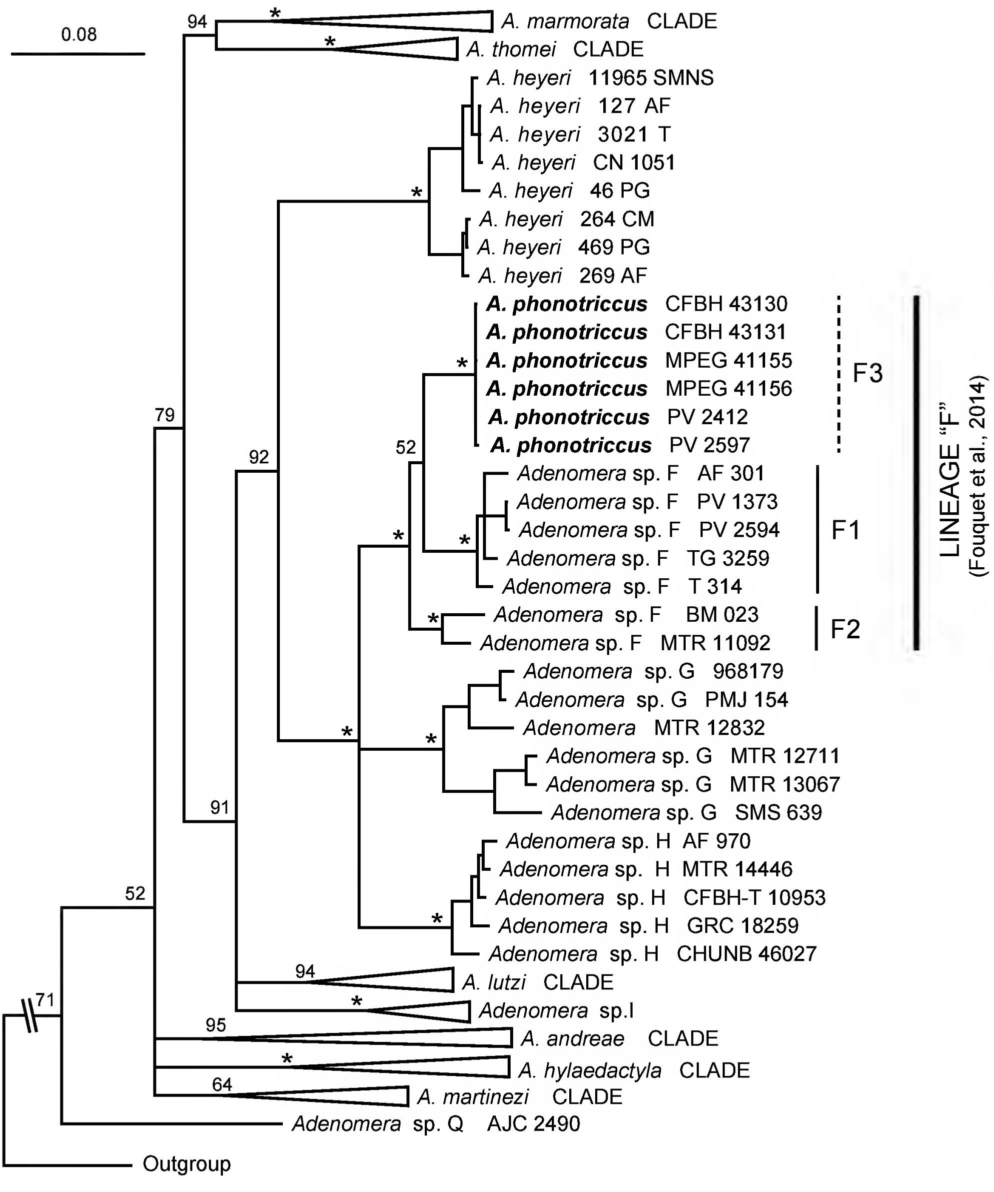

FIG. 6. Phylogeny of *Adenomera* based on 657 bp of the mtDNA COI gene for all individuals from Fouquet et al. (2014) and new sequences for *A. phonotriccus*' type series (vouchers numbers following species names): 50% majority rule consensus tree from Bayesian inference analysis, rooted on *Rupirana cardosoi*. Posterior probabilities (%) are given near the nodes and branch scale is indicated in number of substitutions per site—asterisks (*) indicate maximum probability (100%). For clarity, outgroup relationships are not shown and all clades other than the *Adenomera heyeri* clade are collapsed.

of the central-east part of the state of Pará in association with the west margin of the lower Araguaia River (fig. 6). With respect to subclade F2, we suspect that it may not be conspecific with *A. phonotriccus*, given its distribution range associated with another region in the state of Pará (Xingu-Tapajós interfluve; fig. 6). Therefore, we maintain the original status of unconfirmed candidate species of both subclades F1 and F2 for the moment.

DISCUSSION

The new species named herein represents another case of morphological conservatism, particularly in comparison with the Cerrado species *Adenomera cotuba*, and acoustic divergence between closely related lineages in *Adenomera*. Previous studies had already highlighted the importance of acoustic signals for species differentiation in this Neotropical leptodactylid genus (Angulo et al., 2003; Angulo and Reichle, 2008; Angulo and Icochea, 2010; Carvalho and Giaretta 2013a, 2013b). Interestingly, the unique vocal pattern of *A. phonotriccus*, a species of the *A. heyeri* clade, is shared with an unnamed *Adenomera* species of the *A. andreae* clade, the species "Forest Call II," whose vocalization was described from Tambopata Reserve (Peru) by Angulo et al. (2003)—the species was later referred to as candidate species *Adenomera* sp. C by Fouquet et al. (2014). However, the Peruvian species has toe discs, a feature typical of the *A. andreae* clade, as well as a color feature that is peculiar of this species, a W-shaped marking on the dorsum (Angulo and Icochea, 2010). Therefore, calls with complete pulses in *Adenomera* have evolved independently at least twice in morphologically distinct species belonging to different *Adenomera* clades.

Vocalizations in the *A. heyeri* clade appear to be much more diverse than previously known, and include novel vocal patterns associated with additional undescribed Amazon-associated species (Carvalho et al., in prep.). This reinforces the relevance of acoustic information to species diagnoses in *Adenomera*. Thus, the acoustic characterization of the other lineages pertaining to the *A. heyeri* clade is of high taxonomic interest. It will undoubtedly shed further light on patterns of cryptic species diversity and distribution in the group, given that this clade is widely distributed from the Guiana Shield, across Brazilian Amazonia, and over a vast region of the Brazilian Cerrado. Moreover, the characterization of the major advertisement call patterns could be of help in understanding the evolution of acoustic mating signals in the *A. heyeri* clade and, more broadly, in *Adenomera*.

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APPENDIX 1

Specimens Examined (Brazil)

Adenomera ajurauna—SÃO PAULO: Santo André: Paranapiacaba (AAG-UFU 5024).

Adenomera andreae—AMAPÁ: Serra do Navio (AAG-UFU 5994, 6006-07, CFBH 43259, 43265); AMAZONAS: Manaus (INPA-H 34045, 34048, 34073-74, 34076, 34081-82, 34084-86, 34090); PARÁ: Belém (AAG-UFU 2797-98); Nova Timboteua (AAG-UFU 2788-94).

Adenomera araucaria—RIO GRANDE DO SUL: São Francisco de Paula (holotype: MCP 2421; paratypes: MCP 3208, 3345, 3463, 3672, 3676).

Adenomera bokermanni—SANTA CATARINA: Garuva (CFBH 43152, 43154).

Adenomera cotuba—GOIÁS: Teresina de Goiás (holotype: AAG-UFU 1400; paratypes: AAG-UFU 0808, 1397-99, 1401-04).

Adenomera diptyx—MATO GROSSO: Cáceres (AAG-UFU 5366); Santo Antônio do Leverger: São Vicente (AAG-UFU 1435–38).

Adenomera engelsi—SANTA CATARINA: Florianópolis (holotype: MCP 6415; paratypes: MCP 6379, 6439-40, 7704-05, 8255-56, 8266-67).

Adenomera heyeri—PARÁ: Oriximiná: ESEC-Grão-Pará (MPEG 30099-101).

Adenomera hylaedactyla—ACRE: Cruzeiro do Sul (AAG-UFU 5907-11); Feijó (AAG-UFU 5895-97); AMAZONAS: Manaus (INPA-H 22410-13, 26606-09); São Gabriel da Cachoeira (AAG-UFU 3859-66); RORAIMA: Cantá (AAG-UFU 5540-43).

Adenomera juikitam—GOIÁS: Teresina de Goiás (holotype: AAG-UFU 1406; paratypes: AAG-UFU 0807, 1405).

Adenomera lutzi—RORAIMA: Upper Maú River (INPA-H 6247).

Adenomera marmorata—RIO DE JANEIRO: Bangu (MNRJ 51091, 53817–18, 53820, 54081–82, 55684, 58132–38, 58140–42); Saquarema (MNRJ 76775, 76778–79).

Adenomera martinezi—PARÁ: Novo Progresso: Cachimbo (holotype: MZUSP 73695; allotype: MZUSP 73684; topotypes: AAG-UFU 1515–25).

Adenomera nana—SANTA CATARINA: Jaraguá do Sul (MCP 8149-50); Joinville (MCP 8633); São Bento do Sul (MCP 8751-55).

Adenomera saci—GOIÁS: Alto Paraíso de Goiás (holotype: AAG-UFU 1339; paratypes: AAG-UFU 0108–09, 0762–63; ZUEC 3287).

Adenomera thomei—ESPÍRITO SANTO: Linhares: Povoação (AAG-UFU 6185-86).

APPENDIX 2

Acoustic Definitions and Terminology

Acoustic traits	Brief description
Time domain	
CALL TRAITS	
Note duration (sec)	From initial 10% amplitude (first pulse) to final 10% of note amplitude (last pulse)
Note rise time (%)	Point of maximum amplitude relative to note duration
Note rate (notes/minute)	Note number minus 1, divided by the duration between the onset of first and last notes
PULSE TRAITS	
Pulse duration (msec)	From initial 10% to final 10% of pulse amplitude
Pulse rate (pulses/sec)	Pulse number minus 1, divided by duration of peak-to-peak from first to last pulse of the note
Pulse interval (msec)	From final 10% amplitude of one pulse to initial 10% amplitude of the next
Frequency domain	
CALL TRAITS	
Fundamental frequency (Hz)	Peak frequency of the first harmonic
Dominant frequency (Hz)	Frequency containing the greatest energy in the note
Linear frequency modulation (Hz)	Difference between the peak frequency from final 10% (last pulse) to initial 10% (first pulse) of note amplitude

APPENDIX 3

Information on Sound Recordings Analyzed

Voucher: male, MPEG 41155 (holotype)

Sound file—Adenomera_phonotriccusPalestinaPA2bAAGm661MK2; recorded on Jan. 10, 2018, at 5:58 PM, air 22.0°C.

Unvouchered recording

Sound files—(1) Adenomera_phonotriccusPalestinaPA1aAAGm661MK2; recorded on Jan. 9, 2018, at 6:18 PM, air 27.0°C.

(2) Adenomera_phonotriccusPalestinaPA1bTRC_AAGm670; recorded on Jan. 10, 2018, at 6:18 PM, air 22.8°C.

Voucher: male, field number DT 2133

Sound file—PLPDR 100; recorded on Mar. 6, 2010, at 5:26 PM, temperature not measured.

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